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Some aspects of the mycorhiza problem*

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The roots or underground stems in many families of plants exhibit the constant presence of a symbiotic fungus. Mycorhiza has been described in liverworts and ferns as well as in over twenty families of flowering plants, including gymnosperms, monocotyledons, and dicotyledons. With very few exceptions, mycorhiza is not characteristic of the plants of a whole family, that is, in most families of plants examined, some species have the mycorhiza, and some have not. There are even species of plants in which the presence or absence of the root fungus seems to be determined by external conditions; symbiosis is facultative, so far at least as the phanerogam is concerned.

The identity of the fungus in the mycorhiza has been the subject of many investigations, but has not been definitely determined for more than a very few cases, and even in these not with satisfactory certainty. The chief difficulties in the way of identifying the mycorhiza fungus lies in the fact that the mycelium cannot be readily isolated and made to sporulate. The frequent finding of *Fusarium* forms in cultures of mycorhiza fungus leads to the suspicion of foreign contamination. The spores of *Penicillium* are common in the soil and various moulds frequently appear in cultures even after great pains have been taken to free specimens from adhering soil particles or other foreign matter. All groups of fungi, from bacteria and slime-moulds to Pyrenomycetes and agarics have been declared to form the mycorhiza in different plants by different observers. It is impossible to identify the fungus from the mycelium alone, although recent examinations of forest trees have shown the presence of characteristically colored mycelia which were believed to be connected with sporocarps in the vicinity.

As to the relationship between the fungus and the higher plant

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(commonly called the host although it is not commonly supposed that the relationship is a parasitic one) there have been offered many theories. In 1846 Reissek declared that the root fungus was a normal phenomenon in the life of the plant, like the production of flowers: it is not necessary to the existence of the plant but is produced under certain conditions, spontaneously. Schacht in 1852 and Irmisch in 1853 described the fungus in many orchid roots and rhizomes and concluded that the fungus was not parasitic, but offered no definite explanation of the constant presence of the fungus in the orchid.

In 1877 Pfeffer suggested that as root hairs were absent from the roots or rhizomes bearing fungi, the fungi perform the absorbing function of root-hairs. In 1882, Kamienski, studying *Monotropa*, concluded that the relation between this plant and its root fungus is a mutual symbiosis, and in 1885 Brunchorst ascribed a similar nutritive function to the symbiont of the Papilionaceae. In 1886 Müller inferred from the behavior of the roots of forest trees that the fungus serves to disintegrate the soil. Frank in 1888 thought that the root fungus is of special service to its symbiont in absorbing nitrogen compounds from the soil, or from the humus. It has since been definitely determined that the organisms in the root-tubercles of leguminous plants, as well as other fungi, have the ability to fix atmospheric nitrogen, and this capacity is of sufficient advantage to compensate for any carbohydrate the fungus may obtain from its partner.

There is probably no need to consider, nowadays, some of the earlier theories of spontaneous generation of autonomous organisms within the tissues of the seed plant; or the idea that the fungus-infested tissue is the result of degeneration or the gall of an insect. All the probabilities point to some nutritive relation between two autonomous organisms, including under the concept "nutritive" water and salt relations. However, there is no reason to assume that the mycorhiza has the same significance in all cases.

Our ordinary ideas of mutual symbiosis fail when we come to consider the case of plants entirely free from chlorophyl. The case of *Monotropa* was interpreted by Kamienski as follows: The *Monotropa* derives its organic nutrients from the humus through the intermediation of the fungus, which obtains from the

Monotropa a convenient substratum. Formally, this interpretation explains the relation well enough, but it is not certain that that is all there is to the matter. In several species of *Corallorhiza*, the coral-root orchid, chlorophyl is entirely absent, and the leaves are reduced to a few inconspicuous, sheathing scales. Nevertheless these plants contain large amounts of starch in the underground portions as well as some in the scape and in the floral organs.

We may account for the presence of starch in these plants in the same way as we account for it in the underground portions of a green plant, that is, we may say that it has been condensed from sugar. The real problem in the coral-roots is, how do they get their sugar? Many authors have described these plants and others without chlorophyl as having no stomata; this may have been due to faulty observation, or to *a priori* reasoning from the absence of chlorophyl, or to biased observation. The fact remains that in all species of *Corallorhiza* examined by the writer, stomata are well developed in all parts of the plant, including floral envelope and rhizome. On the latter, the stomata are frequently clogged with earth, but there is no doubt as to their presence. The absence of all absorbing organs has also been declared to be characteristic of these plants. But there is present on each internode of the rhizome a whorl of tiny papillae which are found to bear tufts of fine hairs that may well serve as root-hairs in the absorption of soil water. These trichomes are very delicate and easily destroyed in removing the rhizome from the adhering soil, but they may be easily found by washing the soil off in several changes of water.

Now, the plant having been provided with stomata and absorbing organs, it may be supposed that the organism is prepared to manufacture its carbohydrates in the orthodox fashion, since it has some chromoplasts in the parts above ground. But the area exposed to the light is very small, in comparison with the bulk of the subterranean portion, and the absorbing surface is also very small. Still these facts could not be taken in themselves to preclude the possibility of photosynthesis. A vigorous specimen of *Corallorhiza multiflora* growing in a pine grove was examined for starch by scraping off the skin at several points and treating with dilute solution of iodine in potassium iodide. The plant was covered over with a light-tight box and left this way for several days. On reexamining the subepidermal regions for starch, no difference in the apparent abundance of this substance could be observed. That the plant does not obtain its carbohydrate synthetically I feel convinced.

The only other direction from which it may come is the soil. The constituents of the humus that may yield carbohydrates, the means for their absorption, and the mechanism for their conversion into starch remain to be determined.

The question of the entry of the fungus into the rhizome is another open problem. The seeds of orchids are notoriously indifferent to all efforts to coax them into germination, and without seedlings free from the fungus it is hopeless to find the complete analysis of the relation between the symbionts. In many mycorhizas there have been found hyphal connections between the endotropic mycelium and external mycelia. But in very many cases absolutely no trace of such connection can be found. In *Corallorhiza* the mycelium of the cortical layers frequently sends hyphae singly or in bundles into the trichomes on the papillae, but it is not certain that these hyphae regularly reach the exterior. With the exception of the trichomes, the epidermal cells are uniformly free from hyphae. It has been supposed that the fungus gains entrance through the stomata of the rhizome ; it would be necessary to find seedlings free from the fungus, and stomata through which the hyphae could be seen to pass. I have searched for both and have found neither.

If the orchid is absolutely dependent upon the fungus for its nutrition, how may the seedling develop without the fungus ? The embryo of the orchid seed is undifferentiated, and the nutrients stored within the seed could not carry the plant along very far. But the ripened seeds are ordinarily free from fungus ; at any rate fungal threads are not present in every seed, and it has been impossible to grow from the seeds any fungus that at all resembles the fungus of the mycorhiza. Moreover, the scape, through which any connection between the mycorhiza and the seed would have to pass, is generally quite free from mycelial threads.

The mycorhiza problem is not only of great interest theoretcally, but may have important practical bearings upon the transplanting of trees, reforestation problems, tuberization, nitrification of the soil etc.

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